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THE GENERA OF RHIZOPHORACEAE AND COMBRETACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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RHIZOPHORACEAE R. Brown in Flinders, Voy. Terra Austral. **2:** 549. 1814, "Rhizophoreae."

(RED MANGROVE FAMILY)

Evergreen trees or shrubs of muddy tidal shores, brackish streams or lagoons [or tropical rain forests], often with conspicuous prop or knee roots. Leaves mostly opposite with large, leaflike, caducous stipules. Inflorescences cymose or racemose. Fruit [a dehiscent capsule or] an indehiscent, leathery berry, bearing the persistent calyx. Seeds 1 to many, viviparous in the genera of coastal mangroves. TYPE GENUS: *Rhizophora* L.

A family of about 16 genera and 120 species distributed throughout the tropical and subtropical regions of the world, generally between 25° N. and 25° S. Latitude. *Rhizophora* L., *Bruguiera* Lam., *Ceriops* Arn., and *Kandelia* W. & A., which are the primary components of much of the world's coastal mangrove swamps,[2] are usually thought of as representative

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. The treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present paper. The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References not seen by the author are marked with an asterisk.

The author is grateful for the helpful comments and suggestions of Dr. Wood and for the preserved materials of *Rhizophora*, *Laguncularia*, and *Conocarpus* supplied by Drs. Wood, R. B. Channell, H. H. Iltis, and P. B. Tomlinson, and Mr. David Seligson. The illustration, the work of Dorothy H. Marsh, was supervised by Dr. Wood.

[2] The strange appearance of the mangrove trees with their tangled masses of long prop roots extending down into the water has been recorded by travelers for centuries. Theophrastus (305 B.C.) wrote of mangroves in the Persian Gulf which were "eaten away up to the middle by the sea and are held up by their roots so that they look like a cuttlefish" (Theophrastus, *Enquiry Into Plants* [transl. A. Hort] **1:** 343. 1916). An

of the family, but most of the genera are inhabitants of inland tropical rain forests. A single species, *Rhizophora Mangle* L., occurs in the southeastern United States.

Bentham and Hooker separated the four genera of mangroves from the rest of the family as tribe Rhizophoreae (leaves opposite, style one, endosperm scanty, and embryo macropodous). Wood structure of this tribe, also distinct from that of the inland genera, is characterized by scalariform intervascular pitting, heavy-barred scalariform perforation plates, scanty vasicentric parenchyma, multiseriate rays, and libriform fibers. In addition, only the coastal genera have prop roots and vivipary, apparent adaptations to the littoral habitat. Schimper ignored the morphological similarities among the genera of Rhizophoreae, believing them to be the result of parallel adaptations to the habitat, and related each genus to a different inland genus, a concept not generally accepted.

Embryologically, the genera of Rhizophoraceae differ in several respects from one another (see Mauritzon); each genus shares one or more characters with several different families in the Myrtales. The family is considered most closely related to the Combretaceae on the basis of the unilocular ovary and usually single-seeded fruit. Chromosome numbers of $2n = 36$ and 64 have been reported for the family.

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1. **Rhizophora** Linnaeus, Sp. Pl. **1**: 443. 1753; Gen. Pl. ed. 5. 212. 1754.

Gregarious trees or shrubs inhabiting mud flats of coastal tidal marshes or shallow brackish streams and lagoons, bearing conspicuous, bowed prop roots at the base of the tree and other adventitious roots from the lower branches. Branching opposite, rarely alternate. Leaves petiolate, decussate, simple, entire margined, leathery, persistent, elliptic, oblong to obovate or lanceolate, punctate on the lower (abaxial) surface, stipulate; stipules interpetiolar, leaflike, convolute, surrounding the unexpanded leaf and falling as the leaf expands. Inflorescence axillary, cymose, dichotomously branched with 2–8[–16] flowers, or the flowers solitary, the pe-

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extensive account of *Rhizophora* in early literature may be found in Bowman (1917, pp. 592–603).

duncles and pedicels subtended by connate, 2–4-lobed bracteoles, the flowers borne among [or below] leaves of the current year. Flowers pedicellate [or sessile], regular, bisexual, 4-merous. Sepals 4 (5), ± distinct, valvate in aestivation, persistent, leathery, each with a prominent central longitudinal rib on the inner surface. Petals 4, distinct, alternate with the sepals and folded lengthwise in bud into the depression between the ribs of adjacent sepals, deciduous, leathery, white or yellowish white, lanceolate, equal to or shorter than the sepals, the margins densely villous [or glabrous]. Stamens 8[–12], in 1 whorl, the filaments short or wanting; anthers elongate-deltoid, apiculate, introrse, the inner (adaxial) sides filled with numerous areolae containing pollen and covered by a thin membrane, the apex and 2 longest sides of the membrane becoming free during pollen discharge; pollen oblate-spheroidal, tricolporate, the pores fused laterally forming a zone around the equator, the exine smooth to faintly scabrate, the greatest diameter of the grain about 18μ. Gynoecium syncarpous, bicarpellate; stigmata punctate; style filiform and forked at the apex [or nearly wanting]; ovary 1, the upper portion solid, the 2(–4) locules inferior, each with 2 axile, anatropous ovules pendulous from the apex of the locule and surrounded by spongy tissue, the micropyle upward and outward. Fruit a conical, indehiscent, leathery berry, attached at the base to the receptacle. Seed 1, rarely 2, the other ovules abortive, the apparent placentation parietal due to displacement of the placenta and abortive ovules by the developing seed; seed coat thick, fleshy. Embryo straight, green, in the micropylar end of the endosperm, developing (without a dormant period) into the seedling while still within the fruit on the tree; hypocotyl pendulous, clavate, protruding from the fruit and ultimately disarticulating at the junction with the cotyledons; cotyledons thick, fused into a green tube, protruding from the fruit and withering with it after the seedling has fallen. Embryo sac development of the normal (Polygonum) type; endosperm development of the nuclear type. LECTOTYPE SPECIES: *R. Mangle* L., typified by removal of the remaining Linnaean species of *Rhizophora* to other genera of the Rhizophoraceae. (Name from Greek, *rhiza*, root, and *phoros*, bearing, in reference to the conspicuous prop roots.) — MANGROVE.

A pantropical genus of six to nine species in two sections, RHIZOPHORA and AËROPE Endl.; represented in the Americas by *Rhizophora racemosa* G. F. W. Mey., *R. Harrisonii* Leechman, and *R. Mangle* of sect. RHIZOPHORA (flowers borne among leaves produced the same year, peduncles as long as or longer than the petioles, flowers pedicellate, and stamens eight). Only *R. Mangle*, the red mangrove, a pioneer colonist of silted tidal shores, extends northward into our area to Levy County, on the west coast of Florida, and to Volusia County, on the east, with its greatest development along the low southwestern shore in the region of the Ten Thousand Islands. North of Volusia County the red mangrove does not survive severe winter frosts, and the mangrove swamp is replaced by

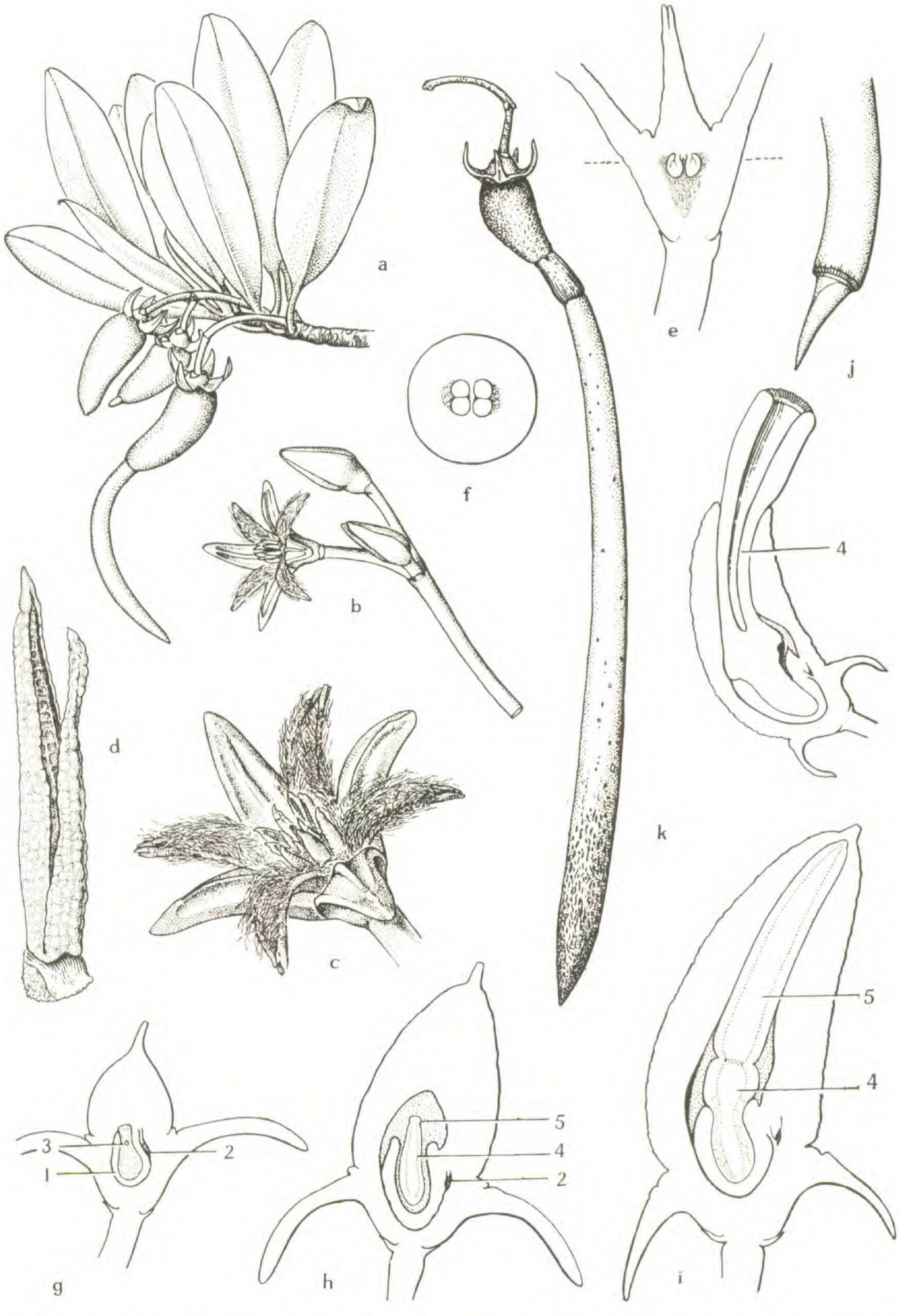

FIG. 1. **Rhizophora.** a–k, *R. Mangle*: a, fruiting branchlet, showing successive stages in development of hypocotyl, × 1/2; b, inflorescence, × 1; c, flower, × 2; d, stamen, inner view, showing mode of dehiscence and pollen areolae, × 16; e, gynoecium and calyx in diagrammatic vertical section, the pendulous ovules surrounded by spongy tissue, × 4; f, two-locular ovary in diagrammatic cross section at level of broken line in "e," × 4; g–j, enlarging fruit in semi-diagrammatic vertical section, showing progressive development from embryo to seedling, × 2 (except j, × 1) — note endosperm (stippled), 1-seed coat, 2-aborted ovule, 3-embryo, 4-cotyledons, 5-hypocotyl (in "j" hypocotyl disarticulated from the cotyledonary tube revealing plumule); k, fruit with seedling showing fully elongated cotyledonary tube and hypocotyl, × 1/2.

salt-marsh vegetation. The mangrove areas of Florida have been estimated to cover more than 1000 square miles (Davis).

The same species, *Rhizophora racemosa*, *R. Harrisonii*, and *R. Mangle*, also occur along the West African coast from Senegal to Angola. *Rhizophora racemosa*, infrequent in the Americas, is the dominant species along the African shore, while *R. Mangle*, the most widespread American species, is less abundant and restricted to dryer ground inland. According to Savory, *R. Mangle*, having a high salt tolerance, is confined in Africa to land which, during the dry season, is flooded only at high tide, so that salt accumulates by evaporation, and which, during the wet season, is not flooded by fresh river water in the delta areas. Differences in distribution of this species on the two continents are difficult to explain on the basis of present information. The species of *Rhizophora* on East African shores are of Indo-Malaysian affinity, the East and West African coasts sharing no species in common. Plants of *R. Mangle* from the Pacific coasts of North and South America and a few Pacific islands (e.g., Fiji, Samoa, Tonga, and New Caledonia) have slightly smaller flowers with shorter styles than those in the rest of the range and have been recognized by some authors as a distinct species, *R. samoënsis* (Hochr.) Salvoza. This distinction is questionable, with at least one character, length of styles, so variable as to make separation of the species on that character impossible (Hou, 1960). There are no positive records of hybrids within the genus.

Environmental factors determining the distribution of the red mangrove include type of soil, salinity of water and soil solutions, tides, water levels, and temperature. *Rhizophora* grows best in shallow water (with a salt concentration at least one-third that of sea water) on deep peat or marl soils free from violent wave action. Recent experiments with *R. Mangle* seedlings in various concentrations of salt solutions show that best development occurs with a salt concentration equalling that of sea water, although seedlings are apparently facultative to a wide range of salinity and are even capable of surviving in fresh water to a limited extent (Stern & Voigt). Plants growing naturally in waters with relatively low salt concentrations, as in parts of the Everglades, tend to be stunted or dwarfed. The high salinity of the water and soil in which *Rhizophora* grows suggested to Schimper that mangroves were physiologically xerophytic and, consequently, had a low rate of transpiration, a much-disputed conclusion. Recent studies indicate transpiration rates are indeed low, but more work is needed on this problem, as well as on all aspects of the physiology of *Rhizophora*.

In addition to *Rhizophora*, the name "mangrove" has been applied to several different genera in at least four other families. *Avicennia* (Verbenaceae), *Pelliciera* (Theaceae), *Sonneratia* (Sonneratiaceae), and *Laguncularia* and *Conocarpus* (Combretaceae) are all "mangroves," characterized by high salt tolerances and the ability to persist along heavily silted shores. The extensive tidal forests which they form are known as mangrove swamps. The swamp formation, an exceptionally uniform one

for the tropics, where diversity is the rule, is generally comprised of three or four genera of mangroves, either in mixed populations, or occupying particular zones in relation to the distance from the shore line. When zonation occurs, *Rhizophora* is in the outermost zone where the substrate is covered by water even at low tide. Other genera, such as *Avicennia* or *Laguncularia*, occur farther inland, where they are only partially flooded at high tide. The tidal action apparently promotes good aëration and gas exchange in the prop roots. Once established, mangrove swamps may play a minor role in accumulation of debris and silt leading to new land formation, but it is doubtful that they are of value in land reclamation, since accumulation of silt usually is not initiated by, but must precede, their establishment.

The red mangrove has both absorptive underground roots and aërial roots. Clusters of superficial, underground, secondary roots appear early in the seedling, taking over the function of the weakly developed taproot. These bear numerous absorptive rootlets, each with a small "rootcap" composed of cells adhering to the rootlet as it grows laterally outward from the parent root. Aërial roots, known as prop roots for their supposed stabilizing action in anchoring the plant to the substrate and generally most abundant on the offshore side of the tree, form along the main stem of the young mangrove about the second year of growth. In older plants additional adventitious aërial roots may form along the lower branches. The surface of the aërial roots is supplied with lenticels which function in maintaining a high oxygen tension in the underground roots submerged in anaërobic mud.

The genera of mangroves in the Rhizophoraceae are notable for vivipary, the germination of the embryo in the seed while the fruit is still attached to the parent plant. In *Rhizophora* normally only one or rarely two ovules develop. Polyembryony is unknown. The growth of more than one hypocotyl from a fruit, implying the occurrence of polyembryony, is due to development of more than one ovule. As the embryo and endosperm grow, the nucellus and inner integument disintegrate, while the outer integument becomes very thick and fleshy, with much vascular tissue, purportedly for transport of nutrition to the embryo. The endosperm, composed of large, translucent cells, is abundant and during development of the embryo grows out of the micropyle, spreading over the outer integument to form an arillode. The presence of absorptive papillae on the endosperm has suggested that the endosperm functions as a placental organ rather than as reserve nutritional material (Bowman, 1917). The embryo develops directly into the seedling without a dormant period. The hypocotyl elongates, piercing through the seed coat and apex of the ovary wall, and is followed by the distal end of the cotyledons, which are fused into a green tube. (See FIG. 1, j.) The plumule lies in the hollow center of the cotyledonary tube. When the hypocotyl is fully elongated, an abscission layer forms at the junction of the hypocotyl and the cotyledons causing disarticulation of the two parts, the hypocotyl and plumule falling into the water or mud below, the cotyledons remaining attached

to the fruit and withering with it. From fertilization to the falling of the seedling is said to occupy nine to ten months. The hypocotyl at the time of fall averages about 25 cm. in length.

The question of how the seedlings become planted has been a controversial one. Early writers (and even many recent ones) believed the hypocotyls plunged vertically downward from the tree, like falling darts, into the mud below where they took root, but more recent observations show that the hypocotyl generally is unable to land erect in the mud because of its slight curvature. It is suggested that the hypocotyls upon falling float, first horizontally, later vertically, until stranded, then gradually become erect through strong upward curvature at the base just above the radicle. The seedlings may float for several months and can retain their vitality up to five months in a dry state, making them capable of being dispersed great distances (Guppy). Regeneration of roots and buds from short pieces of hypocotyl has been reported.

Stellate and H-shaped sclereids are present in practically all parts of the plant. The air-dried bark contains up to 40% tannin, but the tannin is of poor quality, imparting an undesirable red color to leather, and is not used extensively. Large mangrove trees are used in building, particularly as underwater pilings. Small trees are cut in many parts of the world for firewood, and the dense, hard wood is used in making charcoal. Fossil leaves from the Middle Eocene of Georgia, and a fossil calyx from the Lower Eocene of Tennessee have been described as possibly belonging to *Rhizophora*.

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COMBRETACEAE R. Brown, Prodr. Fl. Nov. Holland. 351. 1810, nom. cons.

(WHITE MANGROVE FAMILY)

Shrubs, trees [or woody climbers], mainly of tropical coasts. Buds naked (at least in our genera). Leaves evergreen or deciduous, entire, opposite, alternate, or spirally whorled in dense clusters at the ends of short branches, exstipulate, petiolate or sessile, the blade lanceolate, elliptic, or obovate, often with 2 glands at the base and numerous small pits (domatia) on the undersurface. Inflorescence an axillary spike, terminal panicle, or compact, globose head. Flowers regular [rarely slightly irregular], sessile, bisexual or both bisexual and ♂ in the same inflorescence, usually proterogynous, each subtended by a bract [or the bract absent]. Floral tube glabrous, hairy [or scaly], of 2 distinct parts [of 1 part in the West African *Strephonema*]; lower part adnate to the ovary, tubular or flattened laterally and ± 2-winged; upper part, above the ovary, deeply or shallowly cupuliform, persistent or deciduous; calyx lobes (4)5(6)-merous, deltoid, valvate or imbricate in the bud, hairy [or glabrous] within, sometimes scarcely developed. Petals none or 5 and distinct, greenish white, shorter [longer] than the calyx lobes, deciduous. Stamens 5–10, in 2 whorls, deciduous; filaments scarcely to well exserted; anthers orbicular or cordiform, versatile, 2-locular, longitudinally dehiscent. Gynoecium probably 1-carpellate; stigma capitate or punctiform; style filiform, free from [or adnate to] the upper part of the floral tube, generally surrounded at the base by a nectariferous disc; ovary inferior

[half-inferior in *Strephonema*], 1-locular; ovules 2(–6), anatropous, pendulous from the apex of the locule on slender, generally papillose funiculi. Fruits indehiscent, of various types (scalelike and imbricate in a cone-shaped head, or ellipsoid and laterally flattened, or fleshy and drupelike [or dry with 2–5 broad, papery wings]), composed predominantly of flotation tissue, sometimes also with a sclerenchymatous layer. Seed 1, the other ovules abortive; seed coat membranaceous to thick; endosperm of the nuclear type, scanty or none. Embryo large, straight, often green; cotyledons thick, fleshy, spirally convolute [or plicate]; radicle weakly developed, superior. (Terminaliaceae Jaume St.-Hil. Expos. Fam. 1: 178. *pl. 29.* 1805.) TYPE GENUS: *Combretum* Loefl., nom. cons. (*Grislea* L., 1753, nom. rejic.).

A pantropical family of about 18 genera and 450 species; the largest genera, *Combretum* (250 species) and *Terminalia* (200 species), best developed in the Old World Tropics. The classification of Engler & Diels, with two subfamilies and five tribes, is generally followed. Four genera in two of the four tribes of subfam. Combretoideae are represented in the Southeastern States in southern Florida or the Keys.

The Combretaceae are related to Rhizophoraceae and Myrtaceae and distinguished from them by the unilocular ovary with two to six ovules suspended from the apex of the locule by slender funiculi. The family is characterized anatomically by the common occurrence of intraxylary phloem in the stem, bicollateral veins in the leaves, and the presence at the base of the leaf blade of two flask-shaped cavities containing a multicellular gland. Transparent dots sometimes apparent in the leaves are due to large stellate idioblasts in the mesophyll which contain calcium oxalate crystals. Curious unicellular hairs containing a conical or concave membrane which makes them appear bicellular are widely distributed in the family (cf. Cistaceae). The fruits of practically all genera are well adapted to dispersal by water by virtue of their thick aërenchymatous mesocarp and the ability to float several months in sea water without adverse effect on germination (Guppy). The seed is protected in many genera by a stony endocarp.

Most species are believed to be insect pollinated. The main independent evolutionary tendencies in the family, according to Exell (1954), are elongation of the upper part of the floral tube, leading to pollination by long-tongued insects; congestion of small flowers into spikes or racemes, accompanied by reduction in size of petals; and development of winged fruits, allowing for dispersal by air. Fossil leaves thought to represent *Combretum*, *Conocarpus*, *Laguncularia*, and *Terminalia* are known from the Eocene (Claiborne flora) of Alabama, Mississippi, and Georgia. In addition, a fossil pollen grain of an unknown genus of the Combretaceae has been recorded from the same flora, and a fossil flower related to *Combretum* has been collected from Eocene beds of Tennessee.

Timbers of several species of *Terminalia* are of local importance in construction, and *Bucida* and *Laguncularia* are also used to a limited

extent in the West Indies for building. A tea made from the roasted leaves of *Combretum sundaicum* Miq., a jungle climber native to Malaya, is believed to combat craving for opium. Another climber, *Quisqualis indica* L., Rangoon creeper, $2n = 22, 24$, is cultivated in warm regions for its attractive rose or red tubular flowers. Chromosome numbers of $2n = 22, 24, 26$, and 36 are reported in the family.

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KEY TO THE GENERA OF COMBRETACEAE

General characters: *leaves with 2 inconspicuous glands at the base of the blade; flowers regular, the floral tube mostly of 2 parts, the lower part generally tubular and adnate to the ovary, the upper part cupuliform; ovary inferior, 1-locular; ovules pendulous on slender funiculi; fruit indehiscent, 1-seeded.*

A. Leaves spirally whorled in terminal clusters on short branchlets; fruits ovoid or obliquely ovoid, not conspicuously flattened or winged; petals none; inflorescence racemose; bracteoles on floral tube lacking.
  B. Fruit fleshy, drupelike, ovoid, 20–70 mm. long; calyx lobes well developed, deltoid, deciduous from apex of fruit. . . . . 1. *Terminalia*.
  B. Fruit dry and leathery, obliquely ovoid, 5–10 mm. long; calyx lobes scarcely developed, persistent at apex of fruit. . . . . 2. *Bucida*.

A. Leaves alternate or opposite, not clustered; fruits scalelike or obovoid, laterally flattened, 2-winged.
  C. Leaves alternate; fruits scalelike, imbricate in a cone-shaped cluster; bracteoles on the floral tube none; petals none. . . . . 3. *Conocarpus*.
  C. Leaves opposite; fruits obovoid, solitary; bracteoles on the floral tube 2; petals 5. . . . . 4. *Laguncularia*.

Subfam. COMBRETOIDEAE
Tribe TERMINALIEAE DC.

1. **Terminalia** Linnaeus, Syst. Nat. ed. 12. **2**: 674 (err. 638). 1767; Mant. Pl. 21, 128. 1767, nom. cons.

Trees [rarely shrubs], often with sympodial branching. Leaves deciduous, large, glabrous or with sparse reddish-brown hairs, the apex acute to acuminate, the blade minutely verruculose [rarely with canal-like mucilage cavities] and with 2 inconspicuous glands at the base. Inflorescence a densely flowered axillary spike [rarely a terminal or axillary panicle]. Flowers bisexual or both bisexual and ♂ with the ♂ flowers on the terminal part of the spike, the bisexual flowers on the basal part of the spike, [4]5-merous, subtended by an ovate bract [or bract wanting], both flowers and bracts with dense reddish-brown pubescence. Floral tube greenish white, the lower part narrowly tubular, the upper part shallow, broadly cupuliform, deciduous; calyx lobes [4] 5 [6], deltoid, valvate in bud, densely silky haired within at the base [or glabrous]. Petals wanting. Stamens [8] 10 [12]; filaments exserted; anthers orbicular. Stigma punctiform. Style surrounded at the base by a thickened

5[4 or 6]-lobed disc, the disc densely covered with silky reddish-brown hairs [or glabrous]; ovules 2 (3 or 4). Fruit fleshy and drupelike, ovoid, apiculate at the apex; pericarp of several layers: a fleshy outer one, a fibrous one, a spongy one often containing air cavities, and an irregularly shaped sclerenchymatous inner one, often with pockets of aërenchyma [or the fruit dry, membranaceous, 2–5-winged]. Seed coat thin. (*Adamaram* Adans., 1763, and *Panel* Adans., 1763, nom. rejic.) TYPE SPECIES: *T. Catappa* L. (Name from Latin, *terminalis*, terminal, referring to the leaves clustered at the ends of the branchlets.)

A complex pantropical genus of about 200 species in 20 sections; represented in our area by *Terminalia Catappa* L., Indian almond, $2n = 24$, of sect. TERMINALIA (§ *Eucatappa* Engl. & Diels), in which the fruit is compressed but lacks wings. Native to Polynesia, *T. Catappa* has become naturalized in scattered areas of southern Florida and the Keys. It is widely planted in the tropics as a shade tree, and the young trees, particularly, are admired for their regular, tiered manner of branching. Finger-like growths at the base of the petioles have been interpreted as rudimentary stipules which are drawn inward to an axillary position as the blade of the leaf grows. The seed is edible and is said to have a filbert-like flavor. Its size varies widely, the cultivated races generally having larger fruits than the wild trees (Exell, 1954). The fruits, containing 30–35% tannic acid, find limited use in tanning.

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2. **Bucida** Linnaeus, Syst. Nat. ed. 10. 1025, 1368. 1759, nom. cons.

Trees of tropical coastal hammocks, the young growth clothed with silky reddish-brown hairs; branching sympodial. Leaves evergreen, petiolate [or sessile], obovate to elliptical, mostly without glands at the base of the blade, arranged in spiral whorls in dense clusters at the ends of

branchlets, the branchlets subtended by 2 short spines or without spines. Inflorescence a densely flowered axillary spike [rarely pseudo-umbellate]. Flowers bisexual, 5-merous, subtended by an ovate bract, both flowers and bracts with dense reddish-brown pubescence. Floral tube greenish, the lower part tubular, the upper part shallowly cupuliform, persistent; calyx lobes 5, scarcely developed, valvate in bud, hairy within. Petals wanting. Stamens 10; filaments exserted; anthers cordiform. Stigma punctiform. Style surrounded at the base by a thickened disc. Fruit obliquely obpyriform, not winged or ribbed, the apex bearing the persistent upper part of the floral tube; pericarp composed of a leathery outer layer and a central stony layer with spongy aërenchyma on both sides. Seed coat thin. (*Buceras* P. Br., 1756, nom. rejic.) TYPE SPECIES: *B. Buceras* L. (Name from Latin, *bucida* or *bucaeda,* one who is beaten by a whip made of ox hide; application of the name obscure.)

A tropical American genus of three or four species, with one, *Bucida Buceras*, black-olive, widely distributed from Panama to southern Mexico and in the West Indies, extending northward to Elliott's Key in the Florida Keys.

The genus is very similar to, and perhaps derived from, *Terminalia*, with which it has been united by several authors. The two are easily distinguished in the New World by the difference in the shape and internal structure of the fruit. Exell (1958), although maintaining both genera, has indicated that the distinctive distinguishing fruit characters are lacking in one or two Malayan-Polynesian species of *Terminalia*, which, however, appear unrelated to *Bucida* in any other features. A re-evaluation of the taxonomic relationship of the two genera is desirable, but should be preceded by a comprehensive study of *Terminalia,* a large and morphologically diverse genus which has never been monographed.

In *Bucida Buceras* the fruits are occasionally invaded by a gall-forming mite (*Eriophyes* sp.). The fruits become much elongated, up to 16 cm., and curved or twisted. The name *Buceras*, horn of an ox, is derived from the resemblance of the galls to such horns. Spines derived from lateral buds are present on some plants of this species. Rudimentary stipules, similar to those in *Terminalia Catappa*, have also been reported.

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3. **Conocarpus** Linnaeus, Sp. Pl. 1: 176. 1753; Gen. Pl. ed. 5. 81. 1754.

Shrubs or trees of sandy coasts and hammocks marginal to mangrove swamps [or of borders of tropical rivers], with erect to prostrate, glabrous to densely silver-haired stems. Leaves evergreen, alternate, shortly petio-

late or sessile, the blade elliptic, ovate [or narrowly lanceolate], the apex acute to acuminate or apiculate, the base with 2 raised glands, the lower (abaxial) side with several small pits (domatia), each at the juncture of the midvein with a secondary vein and occasionally also along the outer margin. Inflorescence a globose, many-flowered, conelike head, sessile or pedunculate. Flowers bisexual or both bisexual and ♂ in the same inflorescence, 5-merous, subtended by an ovate, concave bract, the apex of the bract acuminate. Floral tube greenish white, the lower part laterally flattened and 2-winged, the upper part cupuliform, deciduous; calyx lobes 5, valvate in bud, velutinous within. Petals wanting. Stamens 5–8(–10), well exserted, deciduous; anthers orbicular. Stigma punctiform. Style surrounded at the base by a fleshy, velutinous disc. Fruits leathery, laterally flattened, 2-winged, scalelike, imbricate in a conelike cluster; pericarp of thin, leathery outer and inner layers with spongy aërenchyma between. Seed coat thin. LECTOTYPE SPECIES: *C. erectus* L.; typified by the union of the two original species under *C. erectus* by De Candolle, Prodr. 3: 16. 1828. (Name from Greek, *konos*, cone, and *karpos*, fruit, in reference to the conelike head of fruits.)

A genus of two species, *Conocarpus erectus*, the buttonwood, of tropical America and West Africa, and *C. lancifolius* Engl., known only from the river valleys of the northern Somaliland highlands of East Africa. *Conocarpus erectus* reaches northward into Florida as far as Hernando County, on the west coast, and Merritt Island (Brevard County), on the east, occurring inland from the mangrove swamps on ground generally free from inundation by high tides. The alternate, elliptical leaves and fruits clustered into globose, conelike heads are characteristic. It fruits abundantly, but only an estimated 3–10% of the fruits contain seeds (Guppy). The cause of low seed set has not been determined.

The species shows a wide variation in stature and pubescence. Plants range in form from prostrate shrubs in rocky habitats to erect trees on sandy hammocks. The low-growing plants have been recognized by some authors as var. *procumbens* DC. A second, var. *sericeus* DC., has been recognized for plants with silver-haired pubescence which occur in the northern part of the species range. The common glabrous form and the densely pubescent extreme occur mixed in the same population. Both are without distinct geographical range and probably should be regarded only as minor variants. The wood of *C. erectus* is very hard, burning slowly like charcoal, and is prized as a fuel in the West Indies.

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Tribe LAGUNCULARIEAE Engl. & Diels

4. **Laguncularia** Gaertner f. Fruct. Sem. Pl. 3: 209. *pl. 217.* 1805.[3]

Shrubs or trees of coastal mangrove swamps and hammocks, often with small, pencil-like pneumatophores. Leaves evergreen, opposite, leathery, glabrous, oblong to obovate with the apex generally obtuse or retuse, shortly petiolate with 2 glands on the petiole at the base of the blade, the blade with numerous submarginal pits (domatia?) at the ends of the secondary veins. Inflorescence of terminal panicles, or solitary spikes in the axils of leaves. Flowers greenish white, fragrant, bisexual, 5-merous, subtended by a deciduous bract. Floral tube cupuliform to tubular, fleshy, scarcely produced beyond the ovary, inconspicuously ribbed, accrescent, silvery pubescent to glabrous, bearing 2 ovate bracteoles at the apex beneath the calyx lobes; calyx lobes 5, broadly deltoid, imbricate in bud, persistent. Petals 5. Stamens 10; filaments scarcely exserted; anthers orbicular. Stigma capitate. Style surrounded at the base by a thick, flattened disc. Ovules suspended on very short funiculi. Fruit ellipsoid to mostly obovoid, laterally flattened, with 2 thick, spongy wings, densely silvery haired to glabrous, bearing the persistent calyx at the apex; pericarp of leathery outer and inner layers with spongy aërenchyma between. Seed coat thick. TYPE SPECIES: *L. racemosa* (L.) Gaertn. f. (Name from Latin, *laguncularis*, flask- or bottle-shaped, in reference to the shape of the fruit.) — WHITE MANGROVE.

A monotypic genus of the American and West African coastal mangrove swamps. *Laguncularia racemosa*, with opposite leaves, flowers with five small petals, and conspicuous sessile, gray, flask-shaped fruits has a range practically identical with that of the red mangrove, *Rhizophora Mangle*. Where mangrove swamps occur in the Gulf of Mexico region, *Laguncularia* is found growing either mixed with *R. Mangle* and *Avicennia germinans*

[3] *Laguncularia* has been equated, by some authors, with the earlier genus *Horau* Adans. (Fam. Pl. 2: 80. 1763), but, according to Adanson's description, *Horau* has terminal, solitary flowers with no petals, four stamens, and an ovoid, capsular fruit containing a stony seed, characters which do not apply to *Laguncularia*. In addition, Adanson reports that camels browse the leaves of *Horau*, an unlikely fate for an American-West African genus of mangrove swamps. The name *Horau* was taken by Adanson from Kaempfer, who applied it to an East Indian coastal plant with alternate leaves. On this evidence it appears that *Laguncularia* and *Horau* are not synonymous and that *Laguncularia* is in no danger of displacement.

(L.) L. (the black mangrove of the Verbenaceae) or in a distinct zone inland between these genera and *Conocarpus erectus*. It seems to grow best on land at least partly flooded by salt or brackish water at high tide. In Florida, *Laguncularia* occurs as far north as Hernando County, on the west, and Merritt Island (Brevard County), on the east coast.

As with other genera of the family, few observations have been made on the biology of *Laguncularia*. It is known to be semiviviparous, the green embryo generally only piercing the seed coat while in the fruit on the tree, and germination generally not proceeding further until the fruit has fallen. No studies have been made on the origin of the floral tube in Combretaceae, but in *Laguncularia* (and the Old World *Lumnitzera* and *Macropteranthes*) bracteoles present on the tube suggest the possibility that it is partly cauline in origin. The wood of the white mangrove is used extensively in Puerto Rico for fence posts. Attempts are being made there to control cutting and production of *Laguncularia*, so it may become a profitable economic crop.

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